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State–space models of individual animal movement

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Detailed observation of the movement of individual animals offers the potential to understand spatial population processes as the ultimate consequence of individual behaviour, physiological constraints and fine-scale environmental influences. However, movement data from individuals are intrinsically stochastic and often subject to severe observation error. Linking such complex data to dynamical models of movement is a major challenge for animal ecology. Here, we review a statistical approach, state–space modelling, which involves changing how we analyse movement data and draw inferences about the behaviours that shape it. The statistical robustness and predictive ability of state–space models make them the most promising avenue towards a new type of movement ecology that fuses insights from the study of animal behaviour, biogeography and spatial population dynamics.

The importance and challenges of understanding individual animal movement

Movement is a fundamental, yet relatively poorly understood population process. Although population ecology has traditionally concentrated on understanding temporal fluctuations in abundance [1], more recently the focus has shifted to spatially explicit approaches, leading to a greater appreciation of the importance of movement [2]. Moreover, it has been acknowledged that some important population phenomena depend not only on spatial changes in average population density, but also on individual movement behaviour [3,4]. Examples span both marine and terrestrial systems and include the spread of diseases [5–7] and invasive species [8], metapopulation ecology [9,10], home-range characterisation [11] and reserve design [12]. However, interactions between life history, physiology, behaviour and habitat make individual movement an exceptionally complex phenomenon.

Crucially, our understanding of movement is also affected by errors in the observation process. Separating

real biological signals from observation error in data remains challenging and methods that admit uncertainty in movement data when estimating dynamical movement models have been lacking up to this point. The state–space model (SSM, see Glossary) enables this by coupling a statistical model of the observation method with a model of the movement dynamics, which can include effects owing to behaviour and to the environment. Here, we provide an overview of the current use of SSMs in animal movement analysis. We first consider the nature of movement data and other approaches to movement analysis. We then describe how SSMs estimate, predict and provide biological

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Glossary

Behavioural mode: A particular manner of movement that is assumed to be related to a behaviour type. For example, an animal foraging intensively on a productive patch of food might move slowly with much turning.

Hidden Markov model (HMM): A SSM with discrete (i.e. discontinuous) hidden states. Examples include classifying movements as 'transit' or 'resident' and assigning spatial locations to discrete habitat patches. Typically, movement HMMs do not consider observation error on location, but treat the data as the stochastic outcome of a particular behavioural state.

Markov process: A Markov process is a stochastic process in which the probability that the system will be in a particular state in the next time unit is purely a function of its current and past states. This is known as the Markov condition. First-order processes only depend on the current state, whereas higher-order Markov processes incorporate dependencies at greater time lags.

Movement metric: Quantities that might be calculated directly from raw, uncorrected and unprocessed movement data. These include step length (distance between successive locations), speed, the turning angle between locations and so on.

Observation model: In SSMs, this refers to a probabilistic model of the sampling process. In movement data, this might refer to a model that describes telemetry precision or spatiotemporal variation in recapture effort.

Process model: In movement SSMs, a model of the dynamics of the movement through time and space.

Random walk (RW): a mathematical description (often a Markov process) for generating a trajectory in space from a starting position.

State: A quantity that describes a true, but not necessarily known, attribute of a system. For a movement SSM, this might be location, behavioural state, energetic or physiological condition. The variables are time-indexed and might be collected together into a state-vector (e.g. location, behavioural mode and energetic reserves could feasibly be grouped into a state vector).

State–space model (SSM): A time-series model that predicts the future state of a system from its previous states probabilistically, via a process model. The SSM describes mathematically how observations of the state of the system are generated via an observation model.

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inference about movements. Finally, we outline the challenges in future research. We conclude that SSMs provide a powerful analytical foundation for animal movement ecology by simultaneously capturing the essential ecological, physiological and environmental factors driving movements.

The nature of movement data

Empirical data on movement take the form of time-indexed positions of individual animals. Despite the difficulties in predicting and modelling individual movement, it is easy to quantify movement from data in terms of movement metrics (see Glossary), that is, the basic geometric or quantitative properties of the path of an animal. Examples of movement metrics include speed, heading, turning angles between subsequent locations and rates of movement between regions. The values taken by these metrics are partly a result of animal behaviour. For example, over the same amount of time, a bird that is foraging will make shorter movements, with many sharp changes in direction (turning angle), compared with when it makes rapid and directed trips between patches of foraging habitat. Given only movement data from the bird, it is tempting to derive behavioural inferences solely from movement metrics. However, such inferences are confounded by the effects of observation error and changes in environmental conditions.

Animal movement data come from various indirect sources ranging from mark release recapture (MRR) data to individual movements observed *in situ* using electronic tagging and telemetry technology. Advances in technologies such as satellite and Global Positioning System (GPS) transmitters [13], harmonic radar tracking [14] and electronic data storage tags [15] have led to a vast influx of data on the movement of tagged individuals [13] from a diverse range of species in habitats where direct observation is often impossible [16–18]. Each observation method is subject to its own types of error. MRR suffers from variation in the recapture of individuals, owing to biases in sampling schemes (e.g. commercial fishery tag returns might reflect fisher behaviour rather than fish behaviour) or behavioural reactions to observation methods [19,20]. Electronic tagging and telemetry data often suffer from substantial positional imprecision. Light-based geolocation, used for many marine species, relies on estimating position from day length and estimates of noon or midnight. However, diving or cloud cover affects the light measurements, introducing sizable errors [21]. Satellite telemetry is degraded by factors such as satellite coverage and interference [22]. Radio-tracking requires error-prone triangulation procedures for estimating the location of the animal [23]. In some cases the statistical properties of these errors can be assessed from calibration experiments (e.g. by examining reported locations for electronic tags held at known coordinates) [21,22]. Each source of error has the potential to bias our ecological interpretation of movements. For example placing the animal in the wrong location might lead to incorrect conclusions about usage of habitat or of a reserve. Therefore, handling location error becomes central when analysing movement data.

Animal movement analysis: a random walk?

Movement ecology has yet to define a set of standard analytical methods. Furthermore, the complexity of movement data has often led researchers to seek out methods that avoid its complexities rather than embrace them. Awareness of the need to avoid breaking the independence and linearity assumptions of standard biometrical techniques (e.g. significance tests and ANOVA), has meant crucial features of the movement process (such as spatiotemporal autocorrelation) are often treated as nuisance factors [24,25]. Commonly the complexity of the data has been dealt with by subsampling (throwing away) data to reduce autocorrelation between locations [1] and by ad hoc treatments of observation error [26].

As a result, many analyses can be broken down into three stages: error-correction; calculation of movement metrics from corrected paths; and either pattern identification or statistical analysis for biological inference. Such analyses have been used to identify modes of behaviour [27–30], to support hypotheses about search behaviour [31–33], or to classify individuals into subgroups based on their movements [34,35]. Crucially, all error-correction methods [36–38] used in these analyses contain implicit assumptions about how animals move. No matter how simple these assumptions are (e.g. only assuming a maximum plausible travel speed) they might contaminate the error-corrected data and prejudice the results of statistical analysis. For example, Bradshaw *et al.* [39] found that location error could result in incorrect conclusions regarding movement behaviour. Moreover, this compartmentalised approach of error correction, description and ecological interpretation does not separate the effects of observation error from the statistical properties of movement when performing or interpreting statistical analyses [39,40].

As a rejoinder, not all analyses of movement follow this exact recipe. For example, movement data might be sufficiently accurate (e.g. GPS data) for error correction not to be required [41,42]. However, the ability of correlative, pattern-based or hypothesis-testing approaches to directly incorporate underlying ecological mechanisms is limited. Fitting mechanistic models directly to data is a more powerful approach, but more-sophisticated analysis methods are required for this.

State–space models

Recently, the SSM has become more prominent in movement ecology. SSMs bypass the shortcomings of previous approaches by coupling a hypothetical mechanistic model of individual movement (see next section and Box 1), known as the process model, to an observation model. The observation model gives the probability of obtaining a particular observation conditional on the animal's true position, or in SSM parlance, its state. The state simply consists of one or more variables, such as the animal's spatial location, and possibly a behavioural mode, such as foraging, migrating and so on. Essentially, the process model predicts the future state of an animal, given its current state – an assumption known in mathematics as the Markov condition. The observation model then weights these predictions by the likelihood of data, thereby linking the process model to the observations.

The major advantage offered by the SSM approach is that it integrates the three analysis phases – error correction, calculation of metrics and statistical analysis. By explicitly including the observation model, the SSM enables statistical inferences that account for uncertainties in the input data, rather than hiding them in a 'pre-processing' stage. The SSM enables estimation of probabilities of states (e.g. spatial location and mode of movement), process model parameters (e.g. mean speed or turning rate) and observation model parameters (e.g. variance of observation errors). Although joint estimation of observation and process components [43] can be challenging, prior knowledge of observation error can be incorporated from independent studies [22,40,44,45]. This avoids the need to discard imprecise (but costly and valuable) data. Above all, SSMs are flexible. Process models might take environmental or other data as inputs, meaning that the predicted state of the animal is influenced by habitat variables in a biologically realistic way.

SSM methods originated in engineering, but have been applied in a range of disciplines, including population ecology, to estimate population trajectories from imprecise or incomplete survey data [46,47]. Because they are a more powerful way to handle movement data, SSMs have been applied to a variety of situations. Comparing several SSMs, Morales and colleagues [42] found that elk (*Cervus elaphus*) displayed 'encamped' (slow and variable) movements interspersed with 'exploratory' (faster and directed) movements. The encamped mode was associated with open woodland and agricultural habitat. Using state–space analysis of the migration paths of leatherback turtles (*Dermochelys coriacea*), Jonsen *et al.* [48] found distinct diurnal differences in movement rates. These were hypothesized to result from easier daytime navigation or increased foraging on gelatinous plankton by night, a conclusion that might have implications for managing fisheries interactions for this critically endangered species. Similar models highlighted sex-specific foraging areas in grey seals (*Halichoerus grypus*) [49]. SSMs that use non-spatial data (temperature, pressure and salinity) from electronic tags in conjunction with ocean-model output have been used to estimate the locations of Atlantic cod (*Gadus morhua*) [50] and from this, their time spent in marine reserves. Other applications range from estimating movements of tuna [51–53] and butterflies [9] to determining behavioural switches from movement data on pigeons [54] and wolves [55]. Without SSM these analyses would require direct observations of behaviour, which are often impossible to obtain. In addition, artifacts from error in locations would not be differentiated from true movements.

Mechanistic models of individual movement

All movement analyses implicitly or explicitly assume some type of movement model. To be useful as the process model component (Box 1, Equation Ia) of an SSM, the model must relate stochastic animal movement to single movement decisions. Describing a path through space requires either locations, or speeds and directions between locations. For instance, we could model an insect moving along a linear habitat (e.g. a hedgerow) [56] with one of the simplest movement models, the one-dimensional

Box 2. Estimating SSMs

The SSM framework makes it relatively straightforward to specify a biologically meaningful model of animal movement and to accommodate the properties of different data-collection methods. However, fitting these models to data is not straightforward. Here, we describe the main approaches in what is an active area of statistical research.

Maximum likelihood methods

Observation models specify the probability distribution of the data given the states and parameters. Process models specify the distribution of the states, given those in the previous time period and other parameters. Maximum likelihood estimates (MLE) of parameters can be computed, given data and an initial state, by integrating across all possible states. However, tractable MLEs are available only in the following special cases.

Some process models, such as diffusions (Figure 2b) can be solved numerically to integrate across all possible movement paths [9]. If the SSM is linear and the process and measurement errors are Gaussian, then the likelihood is also Gaussian. MLEs can then be calculated analytically using the Kalman filter [70]. This method has been applied to radio telemetry data [62] and to estimate location from light and sea surface temperature [52,63]. Although computationally fast, the normality and linearity assumptions are often violated. However, several extensions have been developed that enable approximate inference in more general cases [62,63].

Another special case in which MLE is often applied is hidden Markov models, in which data are assumed to be generated by an unobserved, discrete-state, Markov process. Applications to electronic tagging and telemetry data generally assume movement data to be free of error and focus on estimating behavioural switches [54,55,61]. However, hidden Markov models can also be used to estimate positions from noisy location data if space is divided into discrete regions (M. Pedersen, MSc thesis, Technical University of Denmark, 2007).

Bayesian Monte Carlo methods

Many SSMs (e.g. the correlated random walk model in Box 1) are nonlinear and non-Gaussian, and obtaining MLEs using standard methods is not feasible. Computer-intensive Bayesian techniques, MCMC [43,45,48] and particle filtering (PF, also called sequential importance sampling, SIS) [50,51,71] provide a viable alternatives (Figure 1). MCMC simulates values of the states and parameters, conditional on previously generated values, until the chain of samples converges to the posterior distribution. PFs simulate samples called 'particles' from the priors on the parameters and states at the first time point. Essentially, a particle represents a random possible combination of parameters and states (e.g. paths, behaviours). Each particle is then projected forward by the process model and weighted at each time point according to its likelihood. The 'fittest' particles (i.e. with higher weights) are selected by the filtering algorithm. These weighted particles form a sample from the posterior.

random-walk. This describes the probability of a decision to move in either direction from the current position or to remain in the same place along a single spatial axis.

We can alter the rules of this simple model to obtain increasingly complex behaviour in two-dimensional space. For instance, instead of directions being equiprobable, the movements might be biased towards the left or right (known as a biased random-walk or random-walk with drift). Mathematically, process models can often be described as continuous- or discrete-time Markov processes. Also, instead of being fixed, movement distances and directions can be drawn from probability distributions.

In simple cases, the distribution of many random walkers can be derived analytically as diffusion models from the

parameters of individual movement, thereby linking individual decisions to population distribution [1]. If we assume discrete behavioural modes, such as foraging versus searching, we can use a separate speed or turning distribution for each (Box 2). One mode might model foraging behaviour with sharp turns and low speeds whereas the other might describe the movements between foraging patches [42]. Switches between modes could also be modelled as functions of time (to capture the effect of age or season), internal state (energetics, life history status) [57] or environmental characteristics (navigational cues, resources, habitat selection) [42]. For example, Priesler *et al.* [58] used Markovian movement models (albeit not SSMs) incorporating a range of habitat features to characterize cyclical movements of elk. Distances to food patches, streams and roads as well as the time of day were all found to effect elk movements.

As with non-statistical behavioural classification techniques (e.g. [59,60]) SSM approaches can be used to fit movement models and simultaneously estimate behavioural modes. For instance, SSM analysis can use the characteristics of the track (e.g. speed or turning angle) to calculate the probability of the animal being in a behavioural mode such as foraging [42,61] (Figure 1). Because of the simultaneous estimation of observation and biological processes, state predictions (e.g. location) can be improved by using a behaviour-dependent model [43]. Moreover, instead of providing simple categorisations of behaviour, the probability of being in a particular mode is estimated (Figure 1 inset) making uncertainty about behavioural categorizations explicit. Additionally, the process model can be constructed so that the behavioural mode of an animal depends on covariates such as habitat type [43]. For example, Ovaskainen [9] modelled butterfly movements with a diffusion model assuming habitat-specific movement and mortality rates and habitat selection at edges between the habitat types (Figure 2).

Estimation and prediction for SSMs

Although the SSM concept has existed for some time, computational issues have, until recently, obstructed its wider application in ecology. The revolutionary increase in the speed of personal computers has facilitated the application of the computationally intensive statistical methods that are often required to fit SSMs. However, the mathematical and computational aspects of SSM estimation methods are not straightforward (Box 2), requiring one of various maximum-likelihood estimation approaches [52,53,55,61–63] or Bayesian simulation [45,51]. An example of the computer-intensive nature of the methods required is that to fit a diffusion process by maximum likelihood to MRR data from a heterogeneous landscape, Ovaskainen [9] had to solve a large matrix equation several million times. Bayesian simulation approaches, such as MCMC [43,45,48,49] or particle filters [51,50] also require hundreds of thousands of simulations of the random quantities in the model to enable reliable inference (Figure 1).

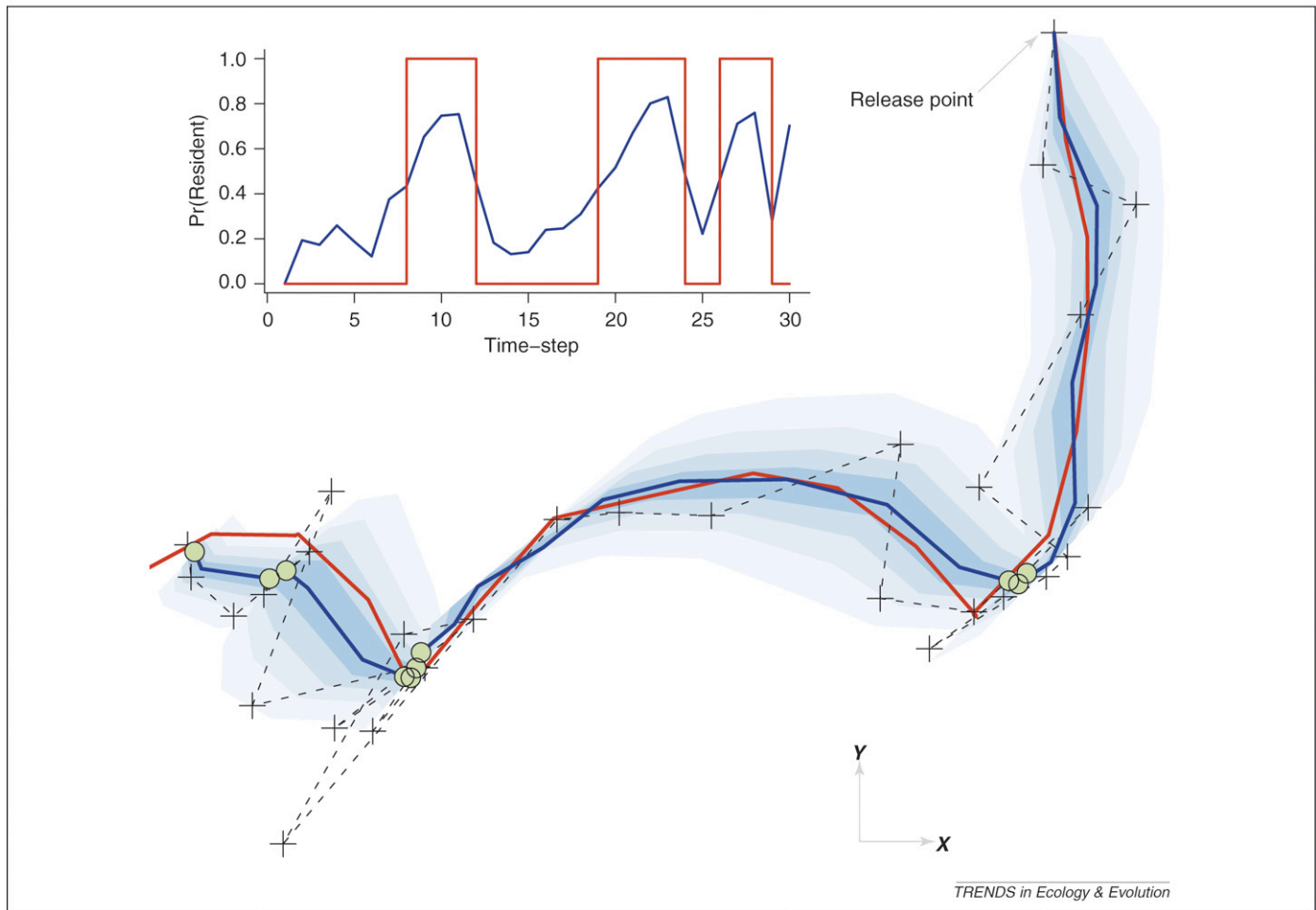Predictions from SSMs take several forms. Having estimated a SSM, it can be used to predict the true path of an

Figure 1. Simultaneous inference of location and behaviour from noisy telemetry data. A hypothetical movement path (red) was simulated from a correlated random walk (Box 1) that switches between two behavioural states – 'transient' and 'resident'. Noisy observations (black crosses) typical of satellite telemetry [22,45] were added. Bayesian particle-filtering techniques (Box 2) were used to estimate movement parameters, the true path and behavioural modes, given moderately informative priors on the parameters. Posterior mean estimates of the true path (dark blue) are shown to vastly improve estimates of the true path. Importantly, uncertainty in the path is quantified (dark to light blue shading indicates 20, 40, 60 and 80% credibility intervals). Locations estimated as being from the resident phase (where the probability of being in resident mode was most likely, Pr[resident] >0.5) are shown as green dots. (Inset) Inferences of behavioural movement mode from the path. The blue line gives the estimated probability of the animal being in resident mode (the probability of transit is simply 1-Pr[resident]); the square red line is the true mode.

animal, to interpolate missing observations or to forecast future movement [47]. In addition, the fitted process model can be used to predict the state of the animal (behaviour and position) depending on covariates such as habitat type or environmental variables, or to predict connectivity of habitat patches (Figure 2b). Because SSMs are based on a mechanistic movement model, they are superior to classical statistical approaches, such as linear models, for purposes of extrapolation, such as predicting movements in novel environments (Figure 2c). Importantly, predicting from the fitted SSM implies fully utilizing the information in the data, via the model, to forecast future movements. A fitted SSM could serve as the basis for simulation. For example, individual-based movement models often use complicated hypothetical decision rules to simulate movements of many individuals, often failing to replicate realistic movement [64]. These could be replaced by simulating from estimated SSMs to generate the expected spatial distribution of the population. This approach, demonstrated by Sibert *et al.* [53], could be useful in a wide range of ecological applications.

Model selection and multi-model inference with SSMs
Determining which hypotheses are better supported by data is central to the practice of science. In a movement context, there are many biological questions to be asked, such as: given noisy observational data, what was the most likely movement path of an animal? What covariates influenced its movement, in what way did they operate, and can we rank their importance? Do different animals move differently with respect to their environment? How many modes of movement are indicated by the data? These questions can be used to generate a series of competing models, and the relative support of these models by the data can be assessed with model selection methods [65]. For example, information criteria [42,66] can be used to select the single best available model by maximising model fit, subject to parsimony. Another option is calculating posterior probabilities of the SSM within the Bayesian paradigm [67]. SSMs fit naturally into the model selection framework, enabling direct comparison and ranking of the explanatory power of the hypotheses embedded in the models. Although model selection methods are not
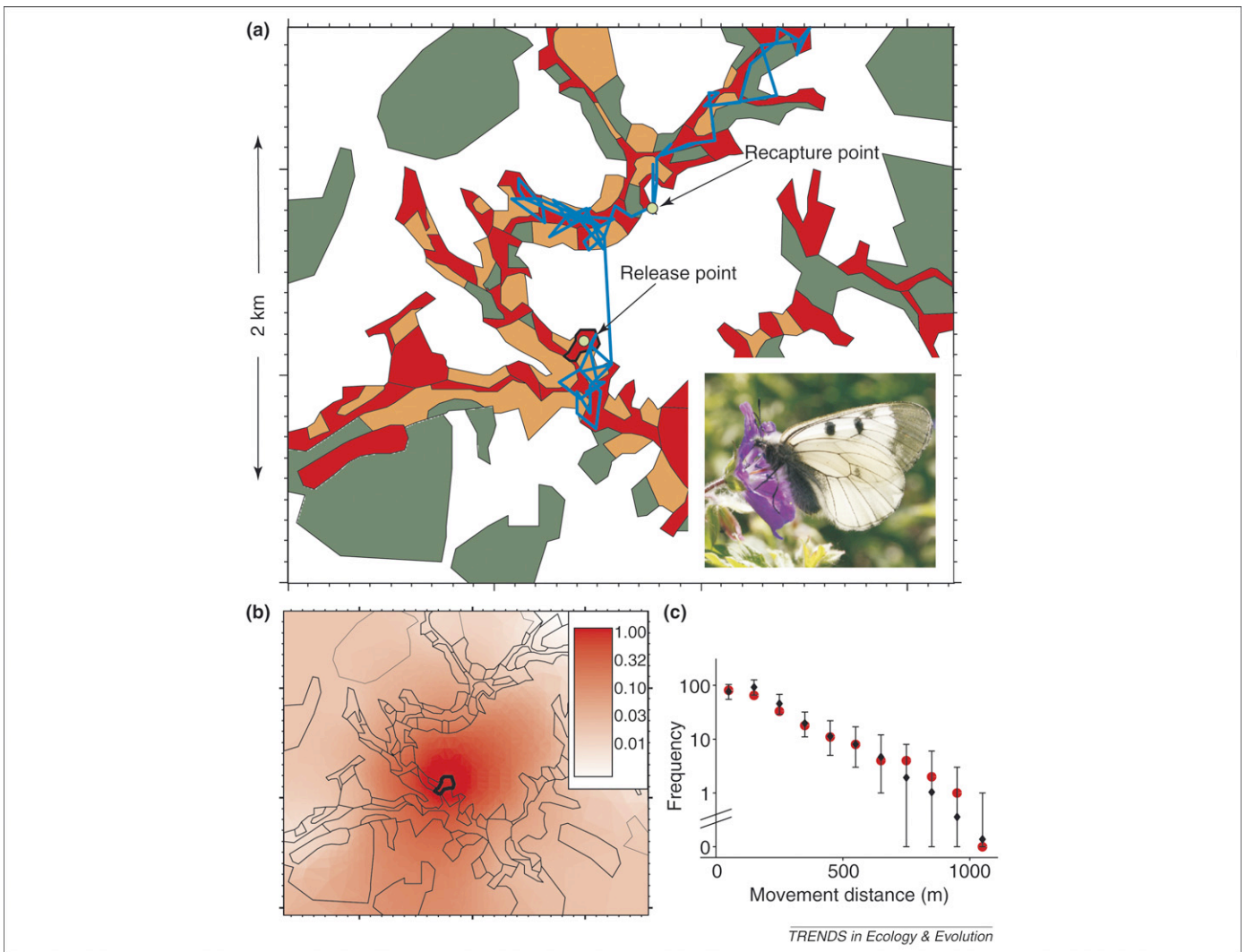
Figure 2. Using state–space models (SSMs) to quantify animal movement in heterogeneous landscapes. Ovaskainen *et al.* parameterised a diffusion-based process model using capture-recapture data from clouded apollo butterflies (*Parnassius Mnemosyne*, photograph inset) acquired from the landscape of panel **(a)** [77]. Different habitat types are shown with different colours, red depicting the breeding habitat, orange semi-open forests, green closed forests, and white cultivated fields. The model includes habitat-specific movement parameters and accounts for edge-mediated behaviour (Box 1). The blue line shows a simulated movement track from the model, from which only few observations (green circles) would be available as capture-recapture locations. **(b)** The fitted SSM can be used to predict movement rates. Here the colour shows the model-predicted probability of butterflies moving from any initial location to the central patch within an individual's lifetime. Without the influence of landscape structure, the probability of movement would be radially symmetric around the central patch. **(c)** Model validation: the model with parameters estimated from landscape (a) correctly predicts (black dots with error bars) independent capture-recapture data (red dots) acquired from a different landscape. Photograph reproduced with permission of Iiro Ikonen.

restricted to SSMs, in the context of animal movement this is a major step forward because it enables assessment the relative support for different biological hypotheses directly from the data. Additionally, SSMs readily lend themselves to combined inference from a set of biologically plausible models, which is more reliable than predicting from a single best model [65]. This can be done via model averaging, using information criteria to weight each candidate model by its relative support, or by fitting algorithms that can sample from multiple models (e.g. reversible jump MCMC [68]). However, such methods have not yet been used in individual movement modelling.

An important application of these methods is that they enable us to understand the relationship of animals to their habitats. We cannot directly observe the majority of habitat use for many marine fish, mammals and seabirds. However, covariates measuring characteristics of these

habitats, such as body and ambient temperature, depth, salinity and light level are often available from electronic tags [13,69]. Although it is unclear *a priori* which covariates are good predictors of preferred habitats, approaching this question by proposing models that include alternative covariates, and then determining the most parsimonious model, can provide a method for determining relationships between the animal and its environment (e.g. [42]). As yet, SSM applications in movement research have not fully used model selection methods to this end.

Where is animal movement modelling heading?
We have outlined four fundamental areas of interest in movement analysis: (i) accounting for observation error; (ii) estimation of movement parameters such as rates and/or direction of movement; (iii) estimation of behavioural modes; and (iv) prediction of (i–iii) on the basis

behaviour, biogeography and population dynamics might eventually become integrated into mechanistic models linking decision-making at the individual level with movement, and, ultimately, with distribution and population structure.

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of environmental or physiological covariates. Of the commonly used techniques for individual movement analysis, the SSM approach is the only candidate that can satisfy all these requirements. Therefore, SSMs are the most likely models to deliver the analytical basis for a synthesis in movement ecology. However, the complexity of the data and the statistical machinery of SSM mean that ecologists researching animal movement will often need to work closely with statistical modelers. As a consequence of this, ecologists will be able to directly include their knowledge in movement models, strengthening the biological foundations of movement analysis.

Although SSMs offer an exciting and significant advance in the study of individual movement, we believe that they have yet to reach their full potential (Box 3). The methods can focus on small-scale individual processes and link these to large-scale population processes. In this way,

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